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# Pilot Whales
# *Globicephala* Lesson, 1828

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## *Genus and Species*

### *Taxonomy*

The genus *Globicephala* was so named (a marriage of Latin "globus" = round ball or globe, and Greek "kephale" = head) because of the characteristic globe-shaped melon. While a number of specific names have been proposed for the genus, van Bree (1971) demonstrated that only two species are recognizable osteologically: *G. macrorhynchus* Gray, 1846, and *G. melaena* (Traill, 1809). Rice and Scheffer (1968), Rice (1977) and van Bree (1971) published lists of recent assignment of other proposed species names. Most recently, Jones *et al.* (1986) proposed a reversion of the specific name for the long-finned pilot whale to its original form, *melas*, and since this usage has gained world-wide acceptance, we shall use it throughout the text.

Subspecific status was proposed for the southern form of *G. melas* in the Atlantic (*G. melaena edwardii*) by Davies (1960), but the validity of this distinction is questionable (Rice, 1977). The nominal species, *G. scammonii* Cope, 1869, from the eastern Pacific is now believed to be a geographical form of *G. macrorhynchus* (Polisini, 1980). Geographic forms of *G. macrorhynchus* also exist in the northwest Pacific Ocean off the coast of Japan (Kasuya *et al.*, 1986a). A northern form is found between latitudes 35°N and 42°N, and a southern form south of this range. The two forms from Japanese waters are segregated both geographically

and thermally (12–24 °C in the north and over 20 °C in the south) and are genetically isolated stocks (Wada, 1986). Both the northeast and northwest Pacific forms appear to be generally larger than the temperate-tropical or southern forms (Polisini, 1980; Kasuya *et al.*, 1986a). Kasuya (1986a) speculated that the larger body size of the northwestern form is an adaptation to the colder waters it inhabits.

### *Evolution*

Barnes (1984) and Barnes *et al.* (1986) proposed the most recent classification of pilot whales within the Delphinidae in the subfamily Globicephalinae. Although the killer whale is also placed in Globicephalinae, Barnes believes that the pilot whale is more closely related to the false killer whale than to *Orcinus*.

The oldest fossil (*Delphinus (phocoenae) uncidens* Lankester, 1864) was found in Pliocene or Pleistocene crag deposits in England. Several fossils have been discovered in North America. A globicephalid fossil was found in a Pleistocene deposit in Florida (*Globicephala baereckeii* Sellards, 1960), and a fossil believed to be a globicephalid was found in late Pliocene strata of California (Barnes, 1976).

### *Common names*

Numerous common names have been assigned to both species of *Globicephala* (Table 1). Both species are referred to as pilot whales (derived from the theory

TABLE 1 A list of common names for the pilot whale

| | *G. macrorhynchus* | *G. melas* |
|---|---|---|
| English | Short-finned pilot whale | Long-finned pilot whale |
| Japanese | Gondo kujira, Siho-goto, Kobire gondo, Tappa naga (northern form), Magondo (southern form), Sibo-goto, Naiso-goto | |
| Mexican | Bufeo | |
| Indians of Washington, USA | Pat-so-ol-qual | |
| Shetland Islands | | Caa'ing whale |
| Faroe Islands | | Grind, Grindhval |
| Danish | | Grindehval |
| Norwegian | | Grinde, Grinzehval |
| German | | Grindwal, Schwartzal |
| French | | Chaudron |
| Uruguayan Spanish, S. America | | Calderon |
| Russian | | Grinda, Chernyi del'fin |



that a leader guides or "pilots" a pod), blackfish, and pothead whales. The common name for *Globicephala melas* is the long-finned pilot whale, while *G. macrorhynchus* is known as the short-finned pilot whale.

## *External Characteristics*

### *Colour pattern*

Pilot whales are predominantly dark grey, brown or black dorsally, except for a light grey saddle behind the dorsal fin. Other light areas more or less apparent are an anchor-shaped patch under the chin, a faint post-orbital blaze, a mid-ventral blaze and genital patch (Figs 1 and 2). Yonekura *et al.* (1980) found the genital patch of long-finned pilot whales to be noticeably lighter than in the sample of the short-finned pilot whales they examined, but variation in colour pattern has not proved a reliable taxonomic character (Evans *et al.*, 1986). However, it may be that variation in the post-dorsal saddle is useful for distinguishing stocks

FIG. 1 A group of long-finned pilot whales near Drake Passage (62° 15′S latitude, 62° 20′W longitude), showing dorsal saddles and post-orbital blaze. (Photo by A. Bowles)

FIG. 2 A group of short-finned pilot whales off Hawaii. (Photo by J. Kilbride, courtesy of Earthviews)

(Evans *et al.*, 1986; Kasuya *et al.*, 1986a, 1988). Davies (1960), Sergeant (1962b), and Norris and Prescott (1961) provided detailed discussions of colour pattern.

Sightings of anomalous white pilot whales on two occasions in the northwest Atlantic indicate the possibility of albinism (Hain and Leatherwood, 1982). The rarity of this condition is emphasized by Bloch (1992) in her review of the Faroe Island drive fishery: only 3 albino whales were recorded in the estimated cumulative catch of over 100 000 pilot whales since 1985.

### *Size and shape*

Pilot whales are among the largest of the delphinids, males reaching 7.2 m in the western North Pacific (*G. macrorhynchus*, Kasuya, 1986a), and 6.17 m in the western North Atlantic (de Kock, 1956). In the northeast Atlantic, in the Faroe Islands area, males have attained a maximum length of 6.25 m (Bloch *et al.*, 1993a). The Indian Ocean stock attains a size intermediate (5.15 m) between the northern and southern Japanese stocks (Kasuya and Matsui, 1984).

In general, the long-finned pilot whale is larger than the short-finned pilot whale (Kasuya and Marsh, 1984; Yonekura *et al.*, 1980). The body shape is considerably more robust than most delphinids, with a large, bulbous melon and



long-based, falcate dorsal fin, set far forward on the body. The flippers are long and sickle shaped, and the tail stock laterally compressed and quite deep dorsoventrally (Fig. 3).

There is a marked sexual dimorphism in size, males being slightly larger at birth and reaching overall greater size by accelerated growth at puberty (Sergeant, 1962b). In the northern Pacific, the largest adult female short-finned pilot whales are shorter than the largest adult males by 2.1 m (Kasuya, 1986a). In the North Atlantic, this difference is 1.06 m (Sergeant, 1962b). Long-finned male pilot whales develop more bulbous melons than do females; however, in a sample of short-finned pilot whales off the Pacific coast of Japan, the size of the melon did not necessarily differ when comparing males and females of the same body length (Yonekura *et al.*, 1980). The large melon of the male may result from a generalized increase in size and not be a separate secondary sexual characteristic (Yonekura *et al.*, 1980). Apparently, there is sexual dimorphism in the flippers and flukes of pilot whales taken in the Faroe Islands area. Bloch *et al.* (1993b) report that male pilot whales there have slightly longer flippers than do females, and longer and wider flukes.

Table 2 lists selected measurements and proportions for comparison of short-finned and long-finned pilot whales. The external characters which have been used most often to distinguish between the two species are length of the pectoral flippers, relative to total body length, and number of teeth (Fraser, 1950; van Bree, 1971). The traditional "rules of thumb" regarding these characters are that the long-finned pilot whale has 9–12 teeth in each row and flippers 1/5 total body length, while the short-finned pilot whale has 7–9 teeth in each row and flippers to 1/6 body length. Recent information from a large series of Atlantic specimens of both species shows considerable overlap in these features, and there appear to be clines rather than distinct groupings as suggested in past literature (personal communication from J.G. Mead of the Marine Mammal Program, Smithsonian Institution). For this reason, both relative flipper length and tooth count are probably unreliable taxonomic characters. The most reliable characteristics for distinguishing between the two species are differences in the skulls (see Table 3 and later in Figs 5 and 6).

### *Weight*

Detailed morphometrics of adult and juvenile pilot whales can be found in Norris and Prescott (1961), Sergeant (1962b), and Yonekura *et al.* (1980). Weights were not reported for these specimens, but Sergeant (1962a) derived a weight–length relationship for long-finned pilot whales in the North Atlantic: $W = 0.000025 \times L^{2.895}$ ($n = 30$), where weight ($W$) is in kg and length ($L$) is in centimetres. Lockyer (1993b) presented weights of long-finned pilot whales taken in the Faroes, and a slightly different weight–length curve: $W = 0.00023 \times L^{2.501}$ ($n = 620$), where weight ($W$) (whales were all weighed whole) is in kg and length ($L$) is in centimetres. This curve is for both sexes,

TABLE 2 Comparison of selected proportions of *G. melas* and *G. macrorhynchus*[a] (southern form)

| Measurement | | *G. macrorhynchus* | | | *G. melas* | | |
|---|---|---|---|---|---|---|---|
| | | *n* | Range | Mean | *n* | Range | Mean |
| Standard length (cm) | M | 13 | 424–491 | 452.6 | 10 | 500–610 | 551.8 |
| | F | 73 | 334–392 | 357.5 | 10 | 405–472 | 440.7 |
| Tip of snout to eye (%) | M | 13 | 8.8–10.7 | 9.5 | 9 | 7.2–9.3 | 8.3 |
| | F | 63 | 8.4–11.0 | 9.7 | 10 | 9.0–10.6 | 9.8 |
| Tip of snout to ant. ins. of flipper (%) | M | 12 | 15.1–17.5 | 15.8 | 9 | 12.6–14.9 | 13.7 |
| | F | 53 | 14.3–19.0 | 17.0 | 10 | 14.4–16.3 | 15.5 |
| Notch of flukes to apex of dorsal fin (%) | M | 11 | 54.2–61.5 | 57.4 | 8 | 52.1–57.8 | 54.6 |
| | F | 47 | 51.3–60.1 | 56.1 | 9 | 48.2–53.1 | 51.2 |
| Notch of flukes to umbilicus (%) | M | 1 | 60.2 | 60.2 | 8 | 58.2–68.0 | 61.2 |
| | F | 16 | 54.8–59.9 | 56.3 | 9 | 57.7–63.2 | 60.3 |
| Notch of flukes to anus (%) | M | 13 | 32.7–36.4 | 34.8 | 10 | 33.9–41.4 | 38.2 |
| | F | 65 | 28.5–35.8 | 33.0 | 10 | 33.8–37.0 | 36.1 |
| Flipper, ant. insertion to tip (%) | M | 0 | | | 9 | 24.1–27.4 | 26.2 |
| | F | 18 | 15.8–18.9 | 16.3 | 10 | 21.9–26.2 | 23.7 |

[a]After Yonekura *et al.* (1980).



TABLE 3 Distinguishing skull characteristics for *G. melas* and *G. macrorhynchus*[a]

| | *G. melas* | *G. macrorhynchus* |
|---|---|---|
| Rostrum | More elongate with rather narrow premaxillae leaving uncovered 1 cm lateral margin of the maxillae | Rather short and broad with broad premaxillae completely covering the maxillae, or leaving a small margin on both sides |
| Teeth[b] | Usually 9–12 in each row | Usually 7–9 in each row |

[a]According to van Bree (1971).
[b]See discussion of teeth in Size and shape section.

which do not differ significantly in weight–length relationship. Kasuya and Matsui (1984) found a nearly identical weight–length relationship to that of Sergeant's (1962b) in their examination of short-finned pilot whales taken by driving fisheries off the coast of central Japan. They presented weights and the weight–length curve: $\log W = 2.8873 \times \log L + \log(2.377 \times 10^{-5})$ $(n = 21)$, where weight $(W)$ is in kg and length $(L)$ is in centimetres.

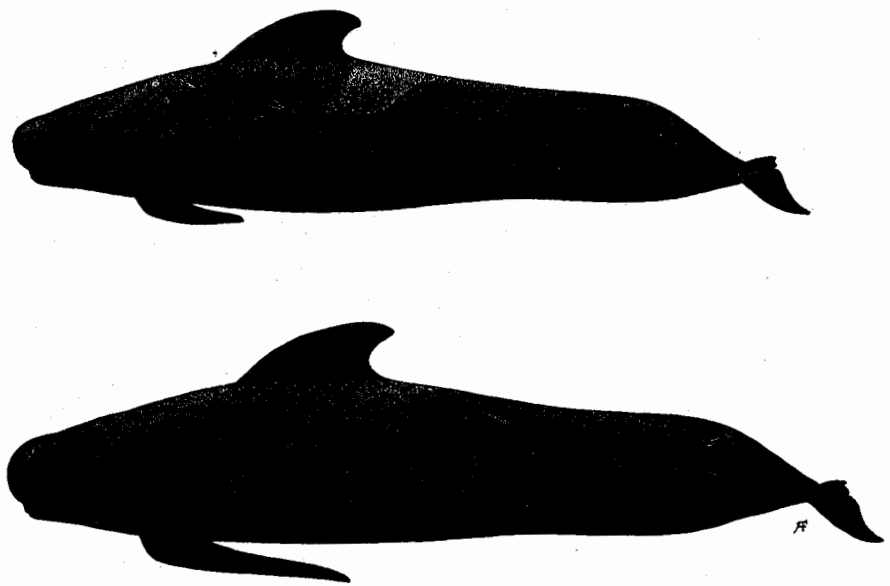

FIG. 3 Comparison of the short-finned pilot whale, *G. macrorhynchus* (upper), and long-finned pilot whale, *G. melas* (lower). (Drawings courtesy of P. Folkens)

## *Distribution*

In general, pilot whales are distributed throughout the world's temperate and tropical oceans, both near shore and in the mid ocean (Fig. 4). The short-finned pilot whale is distributed in the tropical and warm temperate waters of the Atlantic, Pacific and Indian Oceans, while the long-finned pilot whale occurs "antitropically" (Hubbs, 1952; Davies, 1963) in the temperate North Atlantic, and all southern temperate oceans (Rice, 1977). Although the long-finned pilot whale is not known to occur at present in the North Pacific, subfossil material from Japan (Kasuya, 1975) indicates that this species lived in the North Pacific as recently as the tenth century A.D. Polisini (1980) hypothesized that the short-finned pilot whale is in the process of expanding to fill the former range of long-finned pilot whales in the North Pacific.

The distributions of the two recognized species appear to overlap in the temperate waters off the mid-Atlantic coast of the USA (Rice and Scheffer, 1968; Leatherwood *et al.*, 1976; Payne and Heinemann, 1993), off southern Europe and the Azores (Clarke, 1981), South Africa (van Bree *et al.*, 1978), off the coast of Peru and Ecuador (Reilly, 1977; Van Waerebeek and Reyes, 1986), and possibly some parts of the Indian Ocean, and off southeast South America (Ross, 1984; Castello and Pinedo, 1985; J.S. Leatherwood, personal communication).

Marked seasonality in the distribution of pilot whales has been observed in at least five areas: the coastal waters of Newfoundland (Sergeant, 1962a; Mercer, 1975); near New Zealand (Gaskin, 1968, 1972); off southern California (Brown and Norris, 1956; Norris and Prescott, 1961); in the eastern tropical Pacific (Reilly, 1977); and off the coast of Japan (Kasuya, 1975). Along the northeast coast of the USA, there is an apparent seasonal shift of pilot whales from offshore onto the edge of the continental shelf and then northward to Georges Bank (Payne and Heinemann, 1993). In at least two of the above areas (Newfoundland and southern California) the seasonal abundance of pilot whales appears to be correlated with the seasonal abundance of spawning squid (Sergeant, 1962a; Leatherwood *et al.*, 1973; Mercer, 1975). During years of low squid abundance (1983–85), fewer pilot whales were sighted near Catalina Island off the coast of California (C.W. Oliver, personal communication).

In both the coastal and pelagic waters of the eastern tropical Pacific, the density of population centres appears to change seasonally in response to major changes in the current structure of the area (Reilly, 1977). For the rest of the world's oceans, little is known of the details of the distribution of this genus. Leatherwood and Dahlheim (1978) summarized the gross aspects of worldwide pilot whale distribution. Their distribution map is adapted and updated in Fig. 4. Hui (1985) found that the occurrence of short-finned pilot whales was associated with high relief topography in the southern California Bight. Dohl *et al.* (1980) found a seasonal distribution with depth where pilot whales were found in significantly shallower water during winter ($\bar{x} = 375.83$ m) than summer

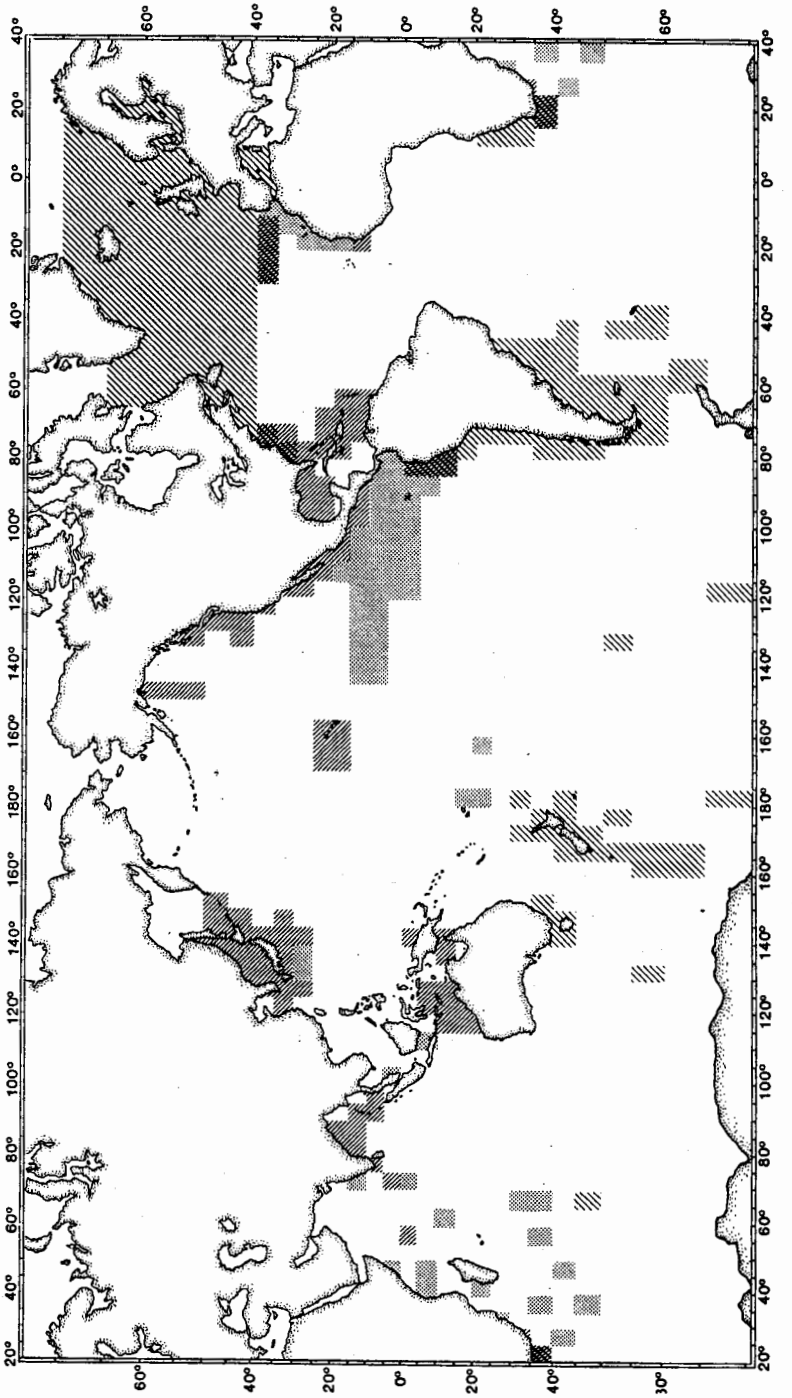

FIG. 4 Distribution of pilot whales (*Globicephala* spp.). *Globicephala melas* approximate distribution represented by leftward slanting parallel lines. *G. macrorhynchus* approximate distribution represented by rightward slanting parallel lines. Areas where the two species overlap are represented by cross-hatching. Dots represent the presence of pilot whales reported but not identified to species. Lined area denotes regions where pilot whales have been observed. Straight borders should not be taken to suggest abrupt limitations of range.

($\bar{x}$ = 798.98 m). However, north of Pt. Conception, Dohl *et al.* (1983) found the occurrences of pilot whales correlated with deeper water (> 1092 m).

## *Internal Anatomy*

### *Skull*

The skull is wide and slightly depressed dorso-ventrally, with a wide and relatively short rostrum (slightly shorter than the braincase). The rostrum is characterized by a notable expansion in width of the premaxillaries. These bones are concave in front of the nares, and, in the mesorostral region, their width is at least 3/4 the total rostrum width (the amount varies between the two species). The relative length of the rostrum decreases with age, with a growth spurt in male short-finned pilot whales at a standard length of 285–375 cm and in females at 195–285 cm (Yonekura *et al.*, 1980). There are also changes with age reflected in relative increases of the orbital width and mesorostral width, and the basal width of the rostrum.

The type skulls of the two species are illustrated in Figs 5 and 6, and a comparison of skull characteristics is presented in Table 3.

### *Postcranial skeleton*

The vertebral formula for the genus is $C_7$, $T_{11}$, $L_{12-24}$, $Ca_{28-29}$ (Tomilin, 1967). Nishiwaki (1972) mentioned specific differences, but their consistent occurrence has not been confirmed. The first 5–6 cervical vertebrae are fused. The phalangeal formula is $I_{3-4}$, $II_{9-14}$, $III_{9-11}$, $IV_{2-3}$, $V_{1-2}$. The ribs are in 11 pairs, 6 pairs are bicipital, and 5 pairs articulate with the sternum on each side. The sternum is in 3–4 parts (Tomilin, 1967).

### *Organs and tissues*

Murie (1874) presented the most complete treatment of pilot whale soft anatomy, but current sources are listed in Table 4.

## *Life History and Population Dynamics*

### *Growth*

Sergeant (1962a) plotted a growth curve for the long-finned pilot whale, but did not linearize the axes or report the parameters of the regression. In another publication, Sergeant (1962b) investigated the morphometrics of growth in more



TABLE 4 Some references on the internal anatomy of pilot whales (*Globicephala* spp.)

| Organ | References |
|---|---|
| Skeleton | Spurrell (1965, 1966), Tomilin (1967), Mead (1975), Nishiwaki (1972) |
| Musculature | Murie (1874), Lawrence and Schevill (1965), Mead (1975) |
| Brain | Murie (1874), Elias *et al.* (1968), Ridgway and Brownson (1984), Haug (1987), Glezer and Morgane (1990), Glezer *et al.* (1993, 1995), Tarpley and Ridgway (1994), Hof *et al.* (1995) |
| Thyroid | Ridgway and Patton (1971) |
| Organ weights | Cowan (1966a,b) |
| Cardiovascular system | Elsner *et al.* (1966), Medway and Moldovan (1966), Olson *et al.* (1967, 1969), de Kock (1969), Ridgway *et al.* (1970), Ridgway (1972) |
| Anatomy, histology, molecular biology and biochemistry | Walen and Modin (1965), Hashimoto *et al.* (1967), Elias *et al.* (1968), Harrison and Young (1969), Pilson (1970), Kulu (1972), Simpson and Gardner (1972), Wedmid *et al.* (1973), Wada (1986), Andersen and Friedrich (1988) |
| Reproduction | Kasuya and Marsh (1984), Marsh and Kasuya (1984), Perrin and Reilly (1984), Donovan *et al.* (1993) |
| Testicle | Desportes (1994) |
| Teeth | Lockyer (1993a) |
| Skull | Oelschlager (1990) |
| Ear | Ketten and Wartzok (1990) |

detail, again for long-finned pilot whales from Newfoundland waters. In their reexamination of life history parameters for long-finned pilot whales, Kasuya *et al.* (1986b) found that after the age of 2.5 years, males grow at a slower but constant rate until about 20 years of age. After the age of 6, the female growth rate declines rapidly and growth stops at 21–25 years.

Growth rates for long-finned pilot whales estimated from some mass strandings in the northeast Atlantic (Martin *et al.*, 1986), and from the Faroe Islands drive fishery (Bloch *et al.*, 1993a) appear to be comparable with those of long-finned pilot whales from the northwest Atlantic (Sergeant, 1962a).

Yonekura *et al.* (1980) plotted growth rates for segments of the body and appendages of the short-finned pilot whale from 211 whales taken in the Taiji drive fishery. They also compared body sizes of whales from their study with those of Sergeant (1962b) (see Table 2). The short-finned pilot whale has a slower growth rate than the long-finned pilot whale and reaches a smaller asymptotic body length. Once again utilizing whales from the drive fisheries of Taiji and Futo, Kasuya and Matsui (1984) derived a mean growth curve which they divided into four phases. The first phase comprises rapid neonatal growth,

(A)

(B)

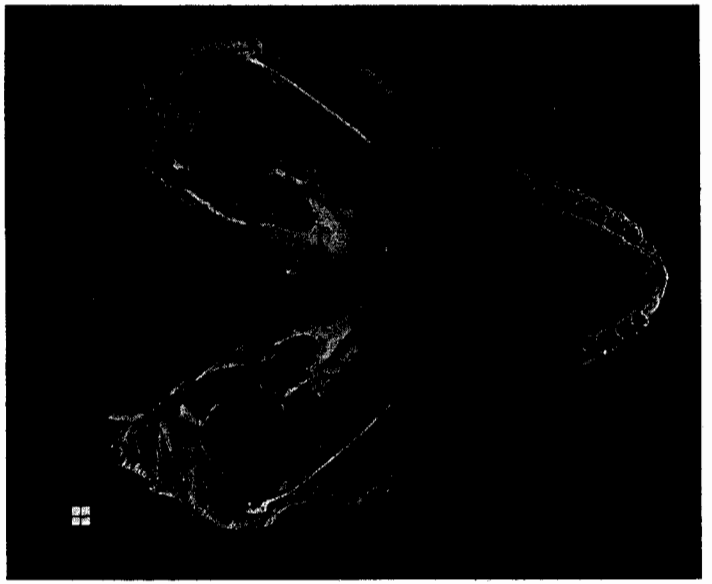

FIG. 5 Type skull of *Globicephala macrorhynchus* (USNM 504396): (A) lateral view and (B) ventral view.



(C)

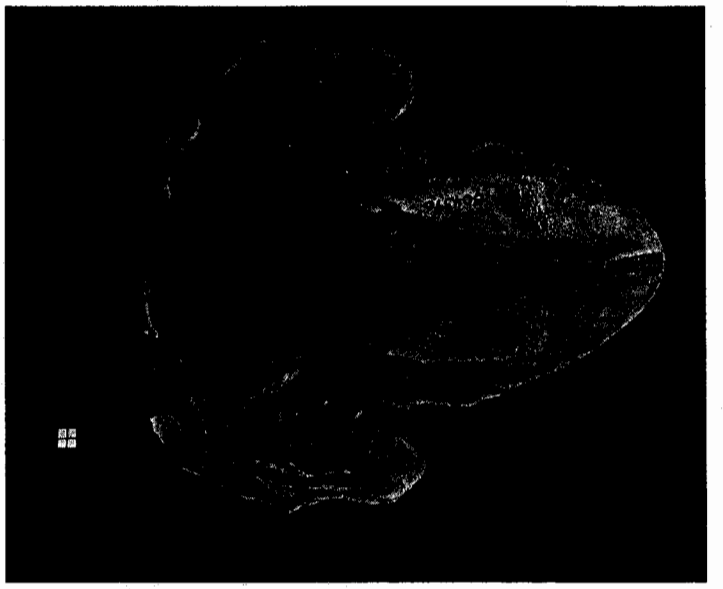

FIG. 5 *Continued* (C) Dorsal view. (Courtesy of C. Potter, USNM; photos by Chip Clark)

which is similar for both males and females and ends at about 1.25 years. The second or juvenile phase is characterized by less rapid but nearly linear growth ending at about the age of first ovulation for females (9 years) and at about 10 years for males. The females tend to be smaller than the males by several centimetres. The third phase encompasses that between puberty and mean asymptotic length. Mean asymptotic length is about 22 years for females. Males undergo a slightly accelerated prepubertal growth followed by a gradual decrease until about the age of 27. The fourth phase is when growth stops.

### *Reproduction*

Reproduction and birth are distinctly seasonal in long-finned pilot whales off Newfoundland, with matings peaking during the period April–May, and calvings peaking during July–September (Sergeant, 1962a). Gestation was calculated to average 15–16 months, and calves are nursed for up to 22 months. Rarely does lactation overlap with pregnancy. The overall reproductive cycle lasts an average of 40 months, with a female producing a maximum of 9 calves during her lifetime.

The long-finned pilot whales off the Faroes have a similar breeding and calving season to those off Newfoundland, with matings extending into July and births through October (Martin and Desportes, 1987). Martin and Rothery (1993)

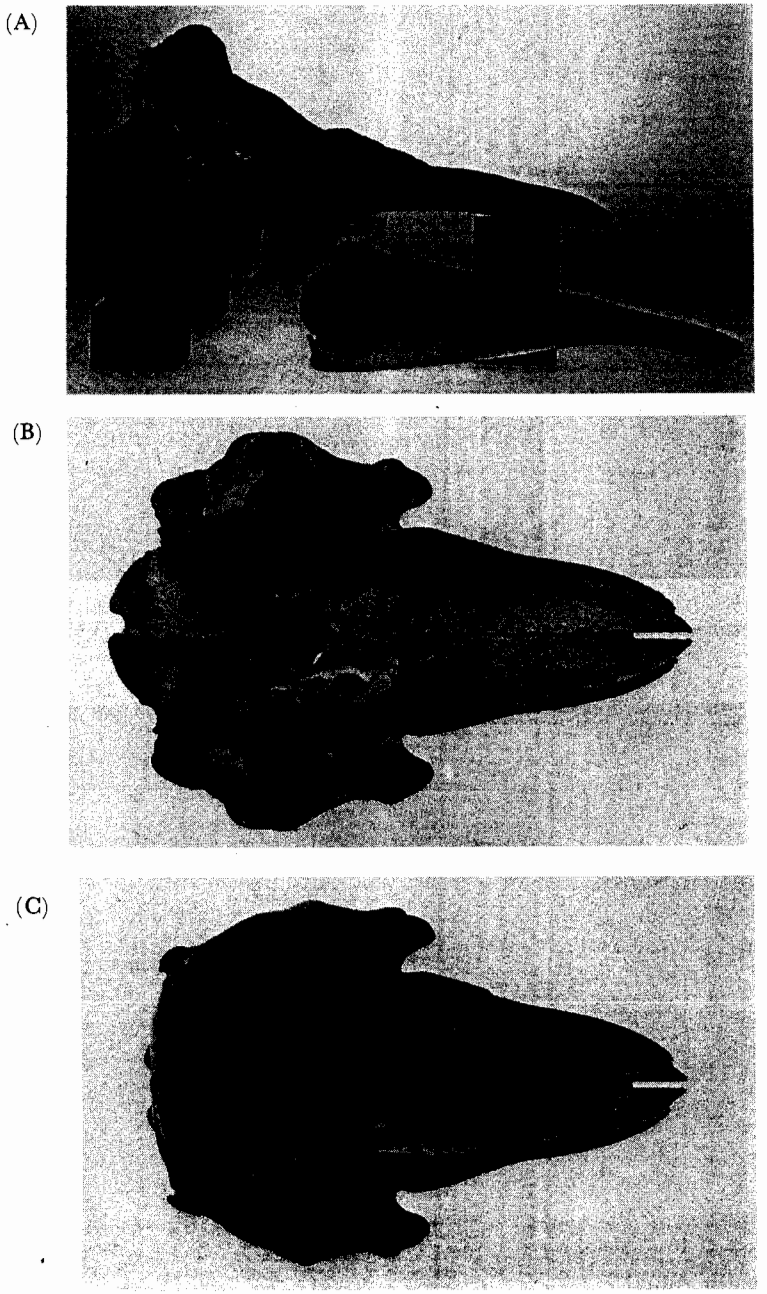


FIG. 6 Type skull of *Globicephala melas* (LACM 28256) from Tasmania: (A) lateral view, (B) ventral view and (C) dorsal view. (Photo courtesy of J. Heyning, Los Angeles County Museum of Natural History)



examined nearly 2000 pilot whales killed in the Faroes drive fishery between 1986–88. Although there may be some biases in this dataset, it is probably the most representative sample available from a pilot whale population. From these data Martin and Rothery (1993) estimated a gestation period of 12 months, significantly lower than estimates from other studies (15–16 months). They believe that previous calculations of gestation period for both long-finned and short-finned pilot whales (Sergeant, 1962a; Kasuya and Marsh, 1984) overestimated gestation length because those studies assumed a linear rather than nonlinear foetal growth rate.

In short-finned pilot whales of the southern form off Japan, reproduction and birth are seasonal, but not distinctly, with a single peak of conception in April–May, parturition during July–August, and a small number of births occurring year-round. The gestation period was calculated to be the same as the longer estimate for the long-finned pilot whale, approximately 15–16 months, with weaning occurring after 3.5–5.5 years. An older female, in her 30s, may nurse her last calf (presumably male calves, because of their older age at maturation) for a much longer time, possibly up to 15 years (Kasuya and Marsh, 1984). This phenomenon, which may demonstrate the tendency of a female to invest more in her current offspring as she becomes less likely to bear additional offspring, is discussed by Marsh and Kasuya (1991).

Kasuya (1986a), and Kasuya and Tai (1993) examined morphology and life history parameters of the northern form of the short-finned pilot whales off Japan and determined that it differs from the southern form in body size (see Section on Taxonomy), dorsal saddle mark (Kasuya *et al.*, 1988) and breeding season. The northern form has a distinctly seasonal breeding pattern, with a peak of conception in September and presumed parturition in December. Kasuya (1986a) speculated that the northern yearlings would be better able to switch from nursing to solid food in the more productive summer/autumn season.

In both species, the females can remain alive long past last ovulation (at least 14 years) (Sergeant, 1962a; Kasuya and Marsh, 1984; and Marsh and Kasuya, 1984). The proportion of postreproductive females is significant in short-finned pilot whales (Kasuya and Marsh, 1984), whereas long-finned pilot whales may remain reproductively active throughout their lifespan (Martin and Rothery, 1993). Long-finned pilot whale females of up to 59 years are reported off the Faroe Islands (Bloch *et al.*, 1993), and one 55 year old female examined by Martin and Rothery (1993) was pregnant.

Table 5 shows a comparison of reproductive parameters for short-finned (both northern and southern stocks) and long-finned pilot whales.

Although the long-finned pilot whale of the western North Atlantic generally is larger than the short-finned, the long-finned pilot whale reaches sexual maturity at a lesser age (northwest Atlantic females, 6 years; northeast Atlantic females, 8 years; males, 12 years) than the short-finned (females, 9 years; males, 16 years). Kasuya and Marsh (1984) speculated that differences in exploitation

TABLE 5 Reproductive and growth parameters of pilot whales (values for males in parentheses)

| | *G. melas*[a] | *G. macrorhynchus* | |
|---|---|---|---|
| | | Northern form[b] | Southern form[a,c] |
| Average length at sexual mat. (cm) | 365 (490) | 390–400 (550) | 316 (422) |
| Average age at sexual mat. (yrs) | 6 (11) 8.3[d] | 9 (17.0–17.5) | 9 (17) |
| Age of oldest individual (yrs) | 59[e] (35.5) | 61.5 (44.5) | 62.5 (45.5) |
| Mean gestation period (months) | 15 (12)[d] | 15–16 | 14.9 |
| Annual preg. rate | 30% | 18–24% | 10% |
| Mean calving interval (yrs) | 3.3 | 4.58–5.70 | 4.8 |
| Average age at weaning (yrs) | 2 | 2.08–2.78 | 2.03 |
| Mean length at birth (cm) | 177 | 185 | 140 |

[a]Sergeant (1962a).
[b]Kasuya *et al.* (1986b).
[c]Kasuya and Marsh (1984).
[d]Martin and Rothery (1993).
[e]Bloch *et al.* (1993a).

pressure or food availability may have influenced the maturation rate of the long-finned pilot whale in the western North Atlantic.

Sergeant (1962a) found that, in the Newfoundland area, approximately 40% of the females were sexually mature during any one year; nearly 40% of these were pregnant.

### *Mortality*

As with other cetaceans, it has proved very difficult to obtain unbiased estimates of natural mortality for pilot whales. The specimen series available (long-finned from the northeast Atlantic, Sergeant, 1962a; Kasuya *et al.*, 1986b; Bloch *et al.*, 1993a; and short-finned from the northwest Pacific, Kasuya and Marsh, 1984) are from fisheries, and are from populations which cannot be assumed to be either stationary in size or stable in age distribution. Consequently, the available estimates represent apparent mortality. Data do not exist to remove the influence of exploitation or recruitment rate changes from any series. However, data from the Faroese drive fishery may provide unbiased representations of sex and age structure within individual pods because usually entire pods were captured.



Given the above limitations, some patterns do emerge. For both species, males appear to have higher mortality rates than females at all ages. Long-finned pilot whales (from the northeast Atlantic) have higher mortality rates (also shown by shorter lifespans) than short-finned pilot whales (from the northwest Pacific). The southern and northern forms of short-finned pilot whales in the northwest Pacific do not appear to have different mortality schedules.

Kasuya *et al.* (1986b) estimated the apparent annual mortality rate of male long-finned pilot whales as about 0.07 below 25 years of age, and 0.15 for the 21–36 year age class. The female mortality rate from this sample was slightly over 0.02 for the below 25 years class, and 0.1 for those 21 years and older. Kasuya and Marsh (1984) reported apparent mortality rates for female short-finned pilot whales of 0.025 for 18–47 year olds, and 0.157 for those aged 45–63 years. For males, they reported apparent rates of 0.044 for 9–30 year olds, and 0.102 for whales aged 27–46 years. Bloch *et al.* (1993a) estimated mortality for northeast Atlantic pilot whales. For males, they show a mean range of 0.0745–0.0817, and for females of 0.0622–0.0737. As in the other forms, males have a consistently higher mortality rate than females.

## *Abundance*

Few quantitatively derived population estimates exist for pilot whales. For long-finned pilot whales fished off Newfoundland, Mercer (1975) used the correlation between the inshore abundance of squid (*Illex illecebrosus*) and pilot whales as a basis for a modified Leslie–DeLury population estimate of approximately 62 000 for 1947, before the start of the intensive fishery which occurred during 1952–1968. Hay (1982) conducted an aerial line-transect survey of long-finned pilot whales in the Newfoundland–Labrador region. His population estimate of long-finned pilot whales is 6731–19 603 for 1980 for over 150 km of the coastal shelf. Sergeant (1986) gave an estimate of 40 000–80 000 long-finned pilot whales for all North Atlantic waters. In 1987 and 1989, joint surveys of the northeast Atlantic were conducted under the auspices of the North Atlantic Sightings Survey (NASS-87 and NASS-89). Buckland *et al.* (1993) analysed the data and estimated 778 000 (CV = 0.295) long-finned pilot whales for most of the north-eastern North Atlantic Ocean.

Clarke *et al.* (1978) compared the numbers of long-finned pilot whales sighted per track mile between ship surveys off Chile in 1958 and 1964. They recorded 13.2 per 100 miles in 1958 and 11.0 per 100 miles in 1964.

Using the line-transect methodology developed for the minke whale population in the Antarctic by the IWC/IDCR (for the years 1976–77 and 1988), Kasamatsu and Joyce (1995) estimated 200 000 (CV = 0.35) long-finned pilot whales for this region.

Several aerial line-transect surveys of short-finned pilot whales conducted off the coast of California during the late 70s–early 80s (Dohl *et al.*, 1980) placed the minimum population at between 200 and 4000, but it is not clear if this represents one or more than one stock.

There have been no systematic studies of home range or migration of individuals of this genus. Opportunistic observations in the southern California Bight have indicated that a pod of 20–30 individuals, identified by scars, unusual marks, etc., lived in the area year-round (Walker, 1975). Following a strong El Niño event in 1982–83, subsequent surveys throughout the 1980s turned up few sightings (Shane, 1986; Forney, 1994), and documented the absence of all but one pod of pilot whales near Catalina Island. Shipboard surveys along the entire California coast using line-transect methodology were conducted in 1991 and 1993 within 550 km of shore (Barlow and Gerrodette, 1996). They documented an apparent return of this stock and calculated an abundance estimate of 1004 (CV = 0.37).

Wade and Gerrodette (1993) estimated abundance of short-finned pilot whales in the eastern tropical Pacific to be 160 200 (CV = 0.138). Their data came from an extensive series of line-transect sightings surveys directed at dolphin populations affected by the tuna purse seine fishery. The cruises searched an area of approximately $19 \times 10^6$ km$^2$, using two ships for 4 months each year, 1986–1990. They noted that a small but undetermined portion of this estimate may apply to long-finned pilot whales in the southeast portion of their study area off Ecuador and northern Peru, where probably the two species are sympatric.

Miyashita (1986) estimated the abundance of short-finned pilot whales off the coast of Japan, using line-transect analysis of sightings data from 1984–1985. He estimated the northern form at 5300 (CV = 0.43) and the southern form at 53 000 (CV = 0.33).

## *Behaviour*

### *Association with other species*

Pilot whales are often seen in association with other cetaceans. In the eastern tropical Pacific, approximately 15% of pilot whale sightings include other cetaceans. They are sighted with bottlenose dolphins (*Tursiops truncatus*) and with tuna–dolphin aggregations (*Thunnus albacares* and *Stenella* spp., Reilly, 1977) and *S. coeruleoalba* (Donovan, 1984). The most common associate in coastal waters is the bottlenose dolphin; pilot whales have been sighted also with common dolphins (*Delphinus delphis*), Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), gray whales (*Eschrichtius robustus*) (Norris and Prescott, 1961; Leatherwood, 1974), fin and sperm whales (*Balaenoptera physalus* and *Physeter catodon*) (Clark *et al.*, 1978; Weller *et al.*, 1996) and with killer whales (*Orcinus orca*) in Faroese waters (Bloch and Lockyer, 1988). Recently, there has been a report of a pilot whale biting and towing a human diver (Shane and Costello, 1993).



### *Group size and social organization*

Pod size appears to vary greatly, with the median size (in the eastern tropical Pacific) being near 10 individuals, while the mean is about 25, with a CV of 2.6. Off southern California, the median pod size is 15, with a mean of 43 and a CV of 2.8 (Reilly, 1977). Shipboard observations in the northwestern Pacific Ocean have found schools of 5–50, with a mean of 20.6 and a CV of 0.62 (Kasuya and Marsh, 1984). Near Newfoundland, pods driven ashore in the years 1951–1959 ranged from 10 to 250 animals, with a mean of 85 (Sergeant, 1962a). Off the Faroe Islands, schools driven ashore between July 1986 and July 1988 ranged from five to 220 animals with a mean of 84 (43 schools represented, $n = 3618$) (Bloch *et al.*, 1990).

Several schools may form loose aggregations to exchange individuals or to mate. These aggregations may also serve a protective function as they become more cohesive in certain situations (Sergeant, 1962a; Kasuya and Marsh, 1984). The lower CV from the estimate by Kasuya and Marsh (1984) may have resulted from their explicit exclusion of aggregations from their estimate of mean school size.

Pilot whales are among the most socially structured of the odontocetes. The short-finned pilot whale is loosely polygynous (Kasuya and Marsh, 1984) like the long-finned (Sergeant, 1962a), with more reproductive females than males per school. Like killer whales, the offspring usually reach sexual maturity in their mother's herd and probably remain there for life; yet there appears to be no inbreeding within a pod. In fact, a high level of outbreeding of male pilot whales has been ascertained through DNA fingerprinting in a study of the Faroes drive fishery (Amos *et al.*, 1993). There is scant evidence to support geographical or social segregation of "bachelor" herds (Kasuya and Marsh, 1984; Amos *et al.*, 1993), and the genetic evidence is supported by field observations of large aggregations of several pods. Therefore, it is likely that the males move between schools when several come together in these temporary aggregations (Amos *et al.*, 1993). Kasuya (1986a) considered older, post-reproductive females to be significant members of the school, contributing to the survival of younger individuals. The social structure revealed by Amos *et al.* (1993) suggests that male pod members may contribute to the survival of their related pod members as well.

Three types of social organization for pilot whale pods off southern California were described by Norris and Prescott (1961) and Brown and Norris (1956); travelling/hunting groups, feeding groups, and loafing groups. The travelling/hunting groups have also been appropriately described as "chorus lines" (Leatherwood *et al.*, 1973) as the animals in these are oriented in a broad rank of up to 2 miles in width, but only a few animals deep. Sexual and age–class segregation also have been observed in chorus lines (Norris and Prescott, 1961). In the

second type of group described, the feeding group, there was sometimes a " . . . general movement of whales in a given direction, but individual animals tended to remain fairly independent of one another" (p. 345). The third type of pod, the "loafing group", was described as an almost stationary aggregation of 12–30 or more individuals, floating at the surface, nearly or actually touching one another. A wide variety of types of behaviour, including mating, was reported to occur in loafing groups.

### *Feeding*

Squids are the predominant food item (Sergeant, 1962a; Mercer, 1975; Hacker, 1986; Gales and Pemberton, 1992; Desportes and Mouritsen, 1993; Nelson and Lien, 1996). Widely observed co-occurrence of pilot whales and squid also supports this (see section on Distribution). Fish are also occasionally consumed. In the western North Atlantic, fish prey species reported are Atlantic cod (*Gadus morhua*), Greenland turbot (*Rheinhardtius hippoglossoides*) (Mercer, 1975). Atlantic mackerel (*Scomber scombris*) may be an important component of the winter diet (Waring *et al.*, 1990). Although squids are the predominant prey around the Faroe Islands, some fish, such as *Argentina silus* and *Micromesistius poutassou*, are taken too. The whales in this region do not appear to select cod, herring or mackerel, although they are periodically abundant (Desportes and Mouritsen, 1993). In captivity, pilot whales prefer squid but sometimes will also accept fish (Kritzler, 1952; Brown, 1960).

The daily feeding rate of pilot whales has been reported as 4.0–5.9% of the body weight, both from examination of wild animals (Sergeant, 1962a) and from observation of captive animals (Brown, 1960, 1962; Gilmore, 1962). Captive animals reportedly consume slightly more than those which Sergeant studied near Newfoundland. An annual consumption rate was extrapolated by Mercer (1975) to be between 15 and 18 times body weight. For an "average" size animal of 3.96 m and 830 kg, this is equivalent to 12 410–14 965 kg of prey per year. Lockyer (1993b) calculated a 1000 kg female of reproductive age would consume 11 300 kg of squid per year.

### *Diving depth and duration*

Both in captivity and in open-ocean training, pilot whales have been observed in order to determine how long and how deeply they can submerge themselves. A captive male was observed underwater for 10 min (Caldwell *et al.*, 1963); a radio-tagged whale remained down for up to 12 min and reached a depth of 45.5 m (Leatherwood *et al.*, 1973). At the onset of darkness, the pattern of respirations and frequency of protracted drives increased. During open-ocean training by the US Navy, one short-finned pilot whale made dozens of dives greater than 300 m, with a maximum measured depth of 504 m. Although the depth-of-dive transmitter was malfunctioning when this whale was sent to a target at 610 m, it is assumed that he made it to this depth because of his past performance and dive time (13 min). This whale's maximum time submerged was 14 min 49 sec (Bowers and Henderson, 1972).



### *Sound production*

Pilot whales are known to produce non-harmonic sounds (including echolocating clicks) and harmonic sounds (Evans, 1967). Studies conducted to determine differences in vocalizations between pods of different regions show that only mean whistle duration is useful for distinguishing between long-finned and short-finned pilot whales (Taruski, 1976) and between regional groups of short-finned pilot whales in the Pacific (Evans *et al.*, 1986). Pilot whales can emit variations of their whistle resulting in "shrill or plaintive cries" when in distressing situations such as strandings, captures, and injuries (Brown, 1960; Evans, 1967; and Alagarswami *et al.*, 1973).

### *Mass strandings*

Both species of pilot whale strand singly and *en masse* worldwide (see Dudok von Heel, 1962; Alagarswami *et al.*, 1973; Brownell, 1974; Goodall and Galeazzi, 1986; and Sigurjónsson *et al.*, 1989, for listings of some mass strandings). Necropsies of animals that have mass stranded do not usually yield evidence of acute infections, whereas singly stranded animals are *usually* characterized by pathological findings (Sergeant, 1982). Brain lesions produced by long-term parasitism may lead to disorientation and stranding of an individual, but whales may also carry a heavy parasite load without obvious symptoms (Medway, 1978).

Hypotheses for causes of mass strandings abound. They include navigational error resulting from reliance on magnetic sensory systems (Kirschvink *et al.*, 1986) (or that induced by the apparent inability of pilot whales to use sonar for simultaneous feeding and navigating) and socially or behaviourally induced stranding. If a whale of extreme social importance or strong filial bond strands due to pathological or navigational problems, others in the pod may strand also and then be unable to remain off the beach once removed due to a secondary social or epimeletic response. This social, or perhaps epimeletic, response was used successfully to keep a pod of long-finned pilot whales from repeated strandings by researchers in New Zealand (Dawson *et al.*, 1985). Because the "distress calls" of the beached young of the pod appeared to evoke a stranding response from the older whales, the younger whales were towed offshore and moored to buoys, an action which lured the older animals back out to sea.

It is likely that a combination of two or more of the possible causes of mass strandings leads to such an event.

## Parasites and Disease

The most common disease in a sample of 55 fishery-killed long-finned pilot whales off Newfoundland was infestation with a parasitic worm of the upper respiratory tract. Every whale was parasitized except a calf with no erupted teeth (Cowan, 1966b). Cowan also found that the incidence of lesions of the myocardium and arteriosclerosis increased in frequency with age in this group.

In their examination of fishery-killed pilot whales from the Faroes, Raga and Balbuena (1993) found a different parasite composition, with stomach worms (*Anisakis simplex*) being the most prevalent parasite. They noted that probably this difference is due to different diets between the areas. They found the prevalence and intensity of infection increased with age, and was higher in males.

Common parasites of pilot whales are "whale lice" (*Isocvamus delphini*), cestodes (*Phyllobothrium delphini*), and nematodes (*Anisakis simplex*). Dailey and Brownell (1972) listed known parasites for both species.

Pathogenic bacteria and viruses have been isolated from stranded and captive pilot whales (*Streptococcus*, *Pseudomonas*, *Escherichia*, *Staphylococcus*, and influenza to name a few), but are not necessarily portents of acute infection. As in humans, these and other bacteria and viruses can exist in the system innocuously, becoming acute when the animal is stressed or otherwise compromised (Buck, 1984; Higgins *et al.*, 1980; Hinshaw *et al.*, 1986). Duignan *et al.* (1995) have shown that a high percentage of pilot whales tested have high titres to morbillivirus, suggesting a high rate of infection in western Atlantic animals.

## Live Maintenance

Capture of long-finned pilot whales for public display has been neither extensive nor as consistent as the take of short-finned pilot whales. Prior to 1973, a small number of long-finned pilot whales were captured off New England. Since then, two stranded specimens from the US east coast were held in captivity for a short time (Reeves and Leatherwood, 1984).

Short-finned pilot whales have been collected in southern Californian, Hawaiian, and Japanese waters for aquaria and oceanaria. During 1966–72, 33 pilot whales were taken off the coast of southern California (Walker, 1975), and 17 have been taken since 1973 (Reeves and Leatherwood, 1984). Two of these resided at Sea World in San Diego, California. During this same time period (1963–72), 20 whales were captured near Hawaii (Reeves and Leatherwood, 1984). The annual mean number of short-finned pilot whales taken alive (for public display) in the drive fishery at Taiji during 1974–84 was about six (Kasuya *et al.*, 1984).



Pilot whales have a high mortality rate in captivity (Walker, 1975). Between 1966 and 1973, animals held for public display had an average annual survival rate of 0.51 (D. DeMaster, personal communication; data are from Walker, 1975, Table 6). Animals that survived for at least 90 days had an average annual survival rate of 0.73 (D. DeMaster, personal communication), which indicates that acclimatization to captivity was a problem in these years. More recent information on survival in captivity has not been published.

### *Activity patterns*

Shurley *et al.* (1969) monitored the daily activity patterns of a healthy, trained captive 4-year-old female short-finned pilot whale from the North Pacific. The mean activity pattern for this individual was described as 54% active waking, 26% inactive alert, and 22% behavioural sleep per 24-hour period. It was noted both that the above states were distributed nearly parallel with gross human activity in the vicinity and that the animal was raised in captivity. Gilmore (1962) reported observations on another captive short-finned pilot whale during 2 hours of behavioural sleep. The young male was seen to interrupt its sleep 83 times during the 2-hour period, taking one breath during each. Eighty of the intervals between interruptions were between 15 sec and 1 min 14 sec, while the remaining were 1 min 45 sec, 1 min 50 sec, and 2 min 30 sec.

Kritzler (1952) discussed activity patterns of newly captive short-finned pilot whales from Florida waters. Four of 46 animals that stranded at St. Augustine Beach were moved to tanks at Marineland of Florida. Initially, these whales were distinctly nocturnal in activity. After a period of months, however, the sole survivor had adjusted his activity to the chronology of his feeding schedule.

Epimeletic (care-giving) behaviour has been recorded for at least one captive short-finned pilot whale; he was observed interacting with a dead Pacific white-sided dolphin (*L. obliquidens*) for half a day. The whale brought the dolphin to the surface repeatedly and interfered when divers tried to remove it from the tank (Caldwell *et al.*, 1963). Cooperative actions have also been observed in terrestrial mammals with a matricentral or matrilineal structure. In odontocetes, these types of behaviour are exhibited particularly by subadult and adult females (Gaskin, 1982).

## Human Effects

### *Directed fisheries*

Long-finned pilot whales have been hunted by man at least since the sixteenth century near the Faroe Islands. The fishery there has continued to the present, with catches in the early 70s at about 1500 per year (Mitchell, 1975a,b) and

increasing during the mid 80s to near 2500 (Hoydal, 1986). When Joensen and Zachariassen (1982) examined catch statistics for this fishery for 1709–1978, they found a pulse of 100–120 years between what they called "really good years", that is, catches between several hundred to several thousand animals. Hoydal (1986) suggested that the historical catch levels have not affected the numbers of whales subsequently caught in the Faroe fishery.

Small numbers of pilot whales have been taken elsewhere in the North Atlantic, in Norway, West Greenland (Kapel, 1975), Iceland, the Irish coast (O'Riordan, 1975), and at Cape Cod (during the late nineteenth–early twentieth centuries), where a drive fishery took 2000–3000 per year (Mitchell, 1975b). The fishery for the long-finned pilot whale at Newfoundland took a peak annual catch of nearly 10 000 in 1956 but declined after the early 1960s (Mitchell, 1975a) and is no longer in operation (IWC, 1992). Exploitation of this species in the Southern Hemisphere has been sporadic and very low (Mitchell, 1975a).

The short-finned pilot whale has been exploited for centuries in the western North Pacific. Kasuya and Marsh (1984) present data from whaling operations for 1948–1980, on both northern and southern forms (although prior to 1965 the figures are an underestimate of the take of the southern form). The small-type whaling vessels (harpoon gun-equipped) off Hokkaido and Sanriku took a mean annual catch of 91 (range = 0–415) of the northern form during 1948–1979. Between 1948 and 1980, drive and harpoon fisheries took a mean annual catch of 302 (range = 0–781) of the southern form at Taiji, Izu and Okinawa. Both fisheries peaked in the late 40s–early 50s, and subsequently declined with a few exceptional years (see Kasuya and Marsh, 1984; Kasuya, 1986b). In recent years, the southern form continues to sustain a higher kill than the northern form. In 1982, the drive fishery at Taiji expanded and harpooning of the northern form was resumed off Sanriku and Hokkaido. Between 1982 and 1985, 1755 whales of the southern form were killed (Kasuya, 1986b), and 519 of the northern form were taken during this same time (Kasuya and Tai, 1986). From 1985 to 1989, Japan took a total of 2326 short-finned pilot whales.

Elsewhere, a small, intermittently active fishery takes around 220 pilot whales per year in the Lesser Antilles in the Caribbean at St. Vincent Island (Caldwell and Caldwell, 1975), and there are indications of a small fishery at St. Lucia Island (Gaskin and Smith, 1977). There is evidence that early whalers took substantial numbers of these whales (Mitchell, 1975a). In the 19th century, whalers of the Azores hunted pilot whales to supplement the reduced sperm whale catch in winter, while American sperm whalers used pilot whales for "practice" hunting (Clarke, 1981). There are no records of directed catches of pilot whales in the Lesser Antilles or Azores since 1986 (IWC, 1988).

### *By-catches*

Coastal fish and squid fisheries that utilize drift and set and drift gill nets, seines, unintentionally catch marine mammals along with their target species. This



problem is worldwide in occurrence, but not all species of marine mammals are recovered or reported in most countries. Therefore, there are probably more pilot whales taken incidentally than are presently documented. Based on preliminary data (and very few first-hand observations), the squid round-haul fishery in southern California waters is estimated to have taken 30 short-finned pilot whales in one year (Miller *et al.*, 1983; DeMaster *et al.*, 1985). In the California drift gill net fishery between 1993 and 1995, the mean annual take of short-finned pilot whales was 20 (Barlow *et al.*, 1997).

On the east coast of the USA, the foreign Atlantic mackerel fishery was responsible for the take of 141 pilot whales in 1988. This fishery was suspended in early May of that year as a direct result of this anomalously high take (Fairfield *et al.*, 1993).

A 1990 workshop to review mortality of cetaceans in passive nets and traps documented an annual kill of 50–100 *G. melas* off the Atlantic coast of France, and 350–750 *G. macrorhynchus* off Japan (Perrin, 1994).

### *Pollution*

A growing threat to the integrity of the marine environment is the all-pervasive problem of pollution. Of particular concern are the organochlorine contaminants such as DDT and PCB, which usually have terrestrial origins. Based upon the current rate of PCB pollution, Reijnders (1989) predicts that within the next century, all of the coastal-dwelling marine mammal species will have felt its deleterious effects.

Long-finned pilot whales off the Faroes, France, UK and the eastern USA appear to be carrying high levels of DDT and PCB in their tissues (Taruski *et al.*, 1975; Alzieu and Duguy, 1979; Gaskin, 1982; Martin *et al.*, 1986; Borrell and Aguilar, 1993). However, those animals examined off the Newfoundland and Tasmanian coasts had very low levels, at least of DDT (Anonymous, 1983; Muir *et al.*, 1988).

There is as well a wide variation in contaminant loads in short-finned pilot whales. High concentrations of DDT and PCB were found in whales off the Pacific coast of the USA in the mid 70s (O'Shea *et al.*, 1980), while low levels were found in whales from the Antilles and off Japan (Gaskin *et al.*, 1977; O'Shea *et al.*, 1980; Tanabe *et al.*, 1987).

Heavy metals such as cadmium and mercury also have been found in pilot whales from the Faroes (Simmonds *et al.*, 1994). Because these contaminants accumulate in tissues over time, older animals tend to have higher concentrations. Although not healthful for the animals carrying them, these pollutants may one day play a role in stock differentiation (Borrell and Aguilar, 1993; Caurant *et al.*, 1993).

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